

The Reproductive Behavior of *Diploptera punctata* (Blattaria: Diplopteridae)

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ABSTRACT

The characteristic courtship behavior of males of *Diploptera* was eliminated by bilateral antennectomy and palpectomy; contact chemoreception was probably an important factor in sexual stimulation of the male.

The females of *Diploptera* normally mate just after emergence while they are teneral. As virgin females increased in age fewer mated when exposed to males. Although females did not mate during pregnancy, after parturition they were courted by males and mated about as readily as one-to three-day old virgin females.

A few one-day old males showed courting behavior; however, the courtship behavior of one- to three-day old males was weak and sporadic and these males usually did not mate. Males four or more days old courted vigorously and mated readily.

The duration of copulation and size of spermatophore produced was influenced by the age of the male and whether or not the male had just mated. Males less than ten days old required longer periods of time to copulate and produced smaller spermatophores than males 15 or more days old. Males which mated twice in succession took more than 35 times longer to complete copulation during the second matings and produced smaller spermatophores.

No evidence of parthenogenesis was observed. Most of the females which mated only once produced two or three litters. The majority of females which mated twice produced three or four litters.

Recently Roth and Willis (1955) published some laboratory observations on the biology of *Diploptera punctata* (Eschscholtz) [= *Diploptera dytiscoides* (Serville), Princis, 1950]. They found that the courting and mating behavior of *Diploptera* in many respects is typical of other cockroaches (cf. Roth and Willis, 1954). The male follows the female, touches her with his antennae and mouthparts and flutters or vibrates his wings in front of or to one side of her. He then turns with his abdomen toward the female and raises his wings about 90°. The receptive female straddles his back while applying her mouthparts to his tergum and he pushes his abdomen under the female's and clasps her genitalia. Once joined the pair assumes the opposed position characteristic of blattids with their heads facing in opposite directions.

While in copula the male transfers a spermatophore to the female. Some time later the female forms an oötheca, containing about a dozen eggs, in a manner similar to oviparous cockroaches but then retracts the oötheca into a uterus or brood sac. Here the eggs develop and increase in size through absorption of water and solids from the female. When embryogenesis is complete, in about 50 days at 29° C., the mature embryos are extruded head first, usually in pairs, from the genital opening and the new born nymphs drop free from the female.

In this paper we present additional observations and some experimental data on the reproductive behavior of this viviparous insect.

One series of experiments was performed to determine the role of antennal and palpal sense organs of the male in courtship behavior. The results are shown in Table I. Only after both antennae and both palpi were removed was courtship eliminated. These results are very similar to those obtained with *Blattella germanica* (L.) (Roth and Willis, 1952); in *Blattella* the males discriminated between the sexes largely by means of contact chemoreception. The males of *Diploptera* did not respond sexually to filter paper on which virgin females had been kept for long periods of time. In *Periplaneta americana* (L.) the males are stimulated by female odor and this odorous material is readily picked up by filter paper or other objects on which virgin females have walked (Roth and Willis, 1952; Wharton *et al.*, 1954). Contact chemoreception was probably an important factor in sexual stimulation of *Diploptera* males.

TABLE I—Effect of Removing Antennæ and Palpi of Male *Diploptera*, on Courting Behavior.

Condition of Male	Number Used	Number Courting Female, ^a (within one hour)	Mean Time (min.) before onset of Courting*
Antennæ intact			
Palpi intact (control)	10	10	1.2
Bilateral palpectomy	10	10	0.3
Unilateral antennectomy			
Palpi intact	10	10	2.8
Bilateral antennectomy			
Palpi intact	20	13	12.5
Unilateral palpectomy	20	12	23.3
Bilateral palpectomy	10	0	—

*From the time the male first touched the female.

Although the fluttering of the male's wings is generally a part of the courtship pattern, it apparently has little or no influence on the acceptance of the male by the female. Eight of ten males which had their wings removed, courted females and mated; the mean duration of courtship lasted only 1.7 minutes before mating occurred.

One unusual aspect of mating behavior in *Diploptera* is the fact that the males normally mate with white teneral females (Roth and Willis, 1955); the only other cockroach in which this has been observed is the oviparous species *Neostylopyga rhombifolia* (Stoll) (Roth and Willis, 1956). In the course of our observations it was noted that many old virgin females would not mate. To check this observation adult females were isolated as they emerged and were kept in 250 ml. beakers. When the female was to be tested for mating, a virgin male one week or more old was placed in the beaker. If the male did not court within a few minutes, he was replaced by another male. The male was removed after one hour if copulation did not occur. The results summarized in Fig. 1 show that a considerably larger number of newly emerged females mated than did the older virgin females. Males courted very young females for an average of seven minutes before copulation ensued, as compared to an average of less than four minutes for females one or several hours old. The female was distended with air as she emerged from the last nymphal skin and at this time was not very responsive to the courting male. The behavior of the male toward such a distended female was somewhat modified. He fluttered his wings slowly and briefly and instead of raising his wings he cautiously slipped his abdomen under the female from the side and attempted to copulate. In some instances the male copulated with a distended female without any preliminary fluttering of wings. From ten to twenty minutes (at 27°C. and 70% R.H.) after emergence the female began to deflate and within an hour deflation was completed; both pairs of wings were expanded and her cuticle was cream colored. When the female reached this stage the male courted her with vigorous fluttering of wings and the female usually responded quickly by assuming a position above the male. Although fewer of the older females mated, those which did, responded just as quickly to courting as the younger ones. A female which did not mate within an hour usually took a defensive attitude toward the male; sometimes she walked away or more often she pressed her sides down against the surface on which she stood seemingly to prevent the male from slipping under her abdomen. In some instances the female aggressively chased the male away.

The behavior of males toward pregnant females was also determined. Pregnant females, 25 to 28 days old, were exposed to mature males. The males courted only four (19%) of the 21 females tested, although all of these males courted subsequently when exposed to day-old virgin females. None of the pregnant females mated and they usually repulsed the males.

It was often observed in the *Diploptera* colony that males courted females while the latter were giving birth and immediately after parturition. Females which had given birth to their first brood less than 16 hours previously were exposed individually to sexually

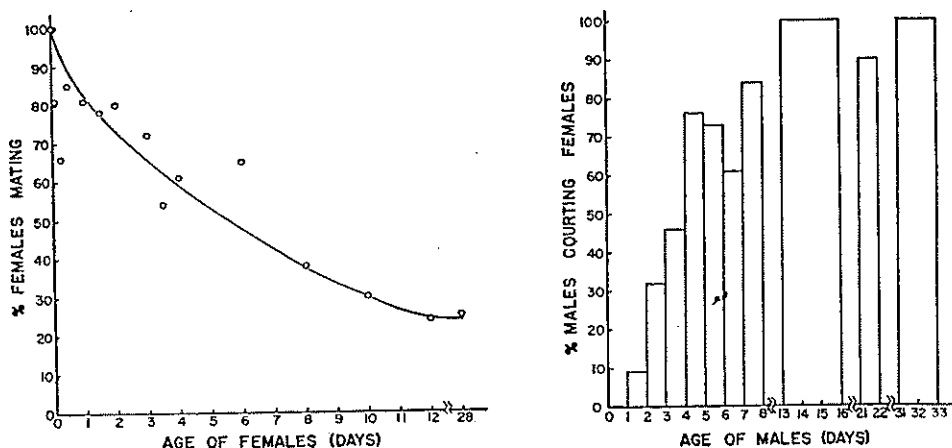


Fig. 1. Effect of age on mating of virgin females of *Diploptera*. The percentage values are based on from 12 to 28 observations; a total of 352 females was used.

Fig. 2. Effect of age on male courting behavior of *Diploptera*. The percentage values are based on from 18 to 35 observations; a total of 249 males was used.

mature males. Sixteen (73%) of the 22 test females mated within an hour indicating that shortly after giving birth the female may mate about as readily as one- to three-day old virgin females.

Though the female of *Diploptera* mated just after emergence as an adult, the newly emerged male showed no sexual activity. Adult males were isolated upon emergence and at various ages exposed to recently emerged (tanned but less than 24-hours old) virgin females. Fluttering of the male's wings within 15 minutes after coming in contact with a female was the criterion for courtship. The results are shown in Fig. 2. No courting activity was observed until the males were at least one-day old. Only a few one- to three-day old males courted females and these males fluttered their wings weakly and sporadically. A larger percentage of males four or more days old courted the females; they fluttered their wings vigorously and continuously, and often raised their wings and extended the hooked left phallomere. Although males less than three days old may court, none were observed to mate; only one three-day old male mated. Males four or more days old mated readily.

The duration of copulation, observed in 31 matings, varied from 24 to 63 minutes averaging 38 minutes. However, the time spent in copula was markedly influenced by the age of the male as shown in Fig. 3 (open circles). Males, less than ten days old required a longer period of time to complete copulation than did males 15 or more days old. Whether or not a male had recently mated also influenced the length of time spent in copula. After a male mated he might continue to court the same female but she discouraged a second mating by raising and moving her abdomen from side to side, and opening her anal segments and closing her genital segments. However, a recently-mated male was observed to mate again with another female. A virgin male 28 days old, mated with a teneral virgin female, and remained in copula 30 minutes, transferring a spermatophore 1.7 mm. long. Subsequently the same male was exposed to another teneral female and after 17 minutes he courted briefly and the pair mated. This mating lasted 25 hours and the spermatophore which was produced was soft and only 1 mm. long. Dissection of the male showed accessory glands completely devoid of opalescent secretion. Several other observations indicated that when the male mated again just after completing an initial copulation the spermatophore produced was small and the mating time was markedly increased. Apparently the male will copulate even though the accessory-gland secretion, necessary for the formation of a spermatophore, has been depleted and he remains in copula while additional accessory gland secretion is formed. Males which mated twice consecutively were fertile even though a small spermatophore was produced during the second mating. Eight of 14 females each mated with a different male produced young (one female had one litter and seven had two

litters each); nine of 14 females mated with the same males just after the first mating also produced young (four had one litter and five gave birth to two litters each).

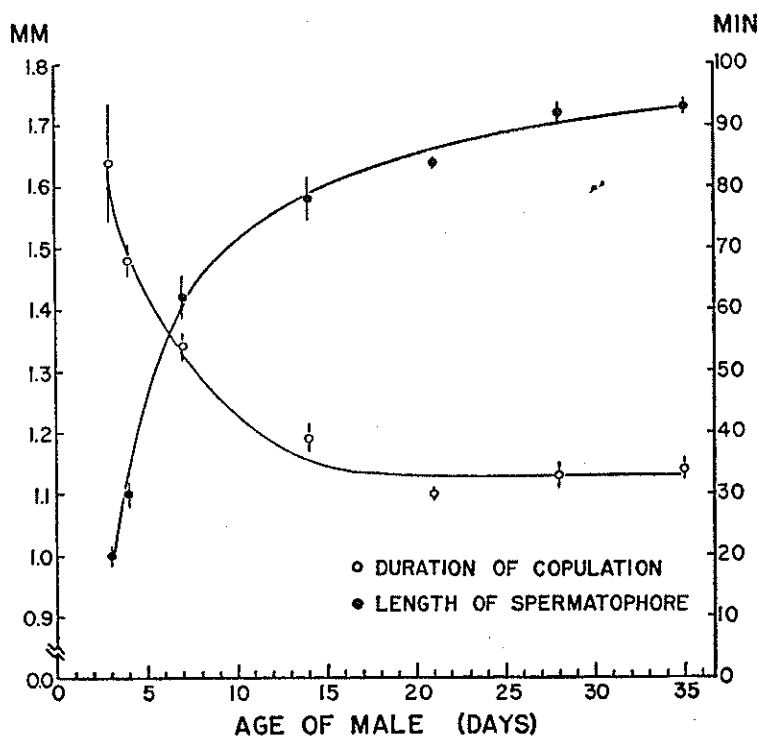


Fig. 3. Effect of age of male on time spent in copula (open circles) and size of the spermatophore (solid circles). Each value is the mean of 10 observations; a total of 70 males was used. Vertical bars represent standard errors.

The size of the spermatophore was influenced to a marked extent by the age of the male. The length of the spermatophore as related to the age of the male is shown in Fig. 3 (solid circles). The average length of the spermatophore of 3-day-old males was 1 mm., while that of males 27 or more days old was 1.7 mm. long. The fertility of 4-day-old males was compared with that of 28-day-old males and the results are shown in Table II; the young males were less fertile than the older males.

TABLE II—Effect of Age of Male at Mating on Fertility of *Diploptera*.

Age (Days) of Male	Number of Litters					Mean No. Litters per Female	No. Used*
	0	1	2	3	4		
4	7	2	1	0	0	0.4 ± 0.22	10
28	1	2	2	4	1	2.2 ± 0.39	10

*Each male was mated to a different female.

The fact that the male which produced a small spermatophore during a consecutive mating was fertile whereas the young male which also produced a small spermatophore was comparatively infertile indicated that spermatophore size was not necessarily a good criterion for fertility in the male. The sperm content of small spermatophores produced by young

males must differ from that of spermatophores of similar size produced by old males during a second mating occurring just after an initial copulation.

TABLE III—Length of Time Spermatophores are Carried by Females of *Diploptera*.

Days After Mating	Number with Spermatophore	Number without Spermatophore or Oötheca	Number without Spermatophore but with Oötheca	Total Number Observed
4	11 (100%)	—	—	11
5	23 (100%)	—	—	23
8	14 (74%)	5 (26%)	—	19
9	30 (40%)	41 (55%)	3 (4%)	74
11	6 (22%)	5 (18%)	16 (59%)	27
12	4 (16%)	5 (20%)	16 (64%)	25
14	0	0	17 (100%)	17
15	0	0	7 (100%)	7
17	0	0	5 (100%)	5

In *Diploptera* the spermatophore was carried by the female until shortly before the oötheca formed. Table III summarizes the results of examining females, at different times after mating, for the presence of spermatophores or oöthecæ. Some females dropped the spermatophore by the eighth day after mating and a small percentage of females had an oötheca in the brood sac by the ninth day. After the twelfth day all of the examined females lacked spermatophores and contained oöthecæ (at 22°C. and 70% R. H.).

TABLE IV—Effect of Mating on Litter Production in *Diploptera*.

Condition of Female	Number of Litters						Mean No. Litters per Female	Average Longevity of Female (days)	Number Used
	0	1	2	3	4	5			
Unmated	10 (100%)	—	—	—	—	—	0	343	10
Mated Once at Emergence	0	3 (7%)	13 (30%)	21 (48%)	6 (14%)	1 (2%)	2.8 ± 0.13	339	44
Mated Twice; at emergence and after first litter	0	1 (5%)	5 (24%)	6 (28%)	8 (38%)	1 (5%)	3.1 ± 0.22	350	21
Mated Twice; at emergence and after second litter	0	0	1 (11%)	5 (56%)	3 (33%)	0	3.2 ± 0.22	318	9

The effect of mating on litter production is shown in Table IV. The unmated female did not produce any young although oöthecæ were formed. No visible development of unfertilized eggs was observed. Most of the females which mated only once produced two or three litters. The majority of females which mated twice produced three or four litters, resulting in a slight, insignificant increase in the mean number of litters per female as compared with females which mated only once. There was little difference whether the second mating occurred after the first or second litter.

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DISCUSSION

L. G. MONTEITH. The recognition of the female by the male seems to be largely through chemotactic rather than olfactory stimuli.

L. ROTH. Yes. Removing the antennæ does not eliminate courting providing the palps are intact. Only after both antennæ and palps are removed is male courtship eliminated. Also contact with the female seems to be necessary for initiation of courtship.

M. W. PROVOST. Does the male mature earlier than the female in this species?

L. ROTH. Yes. At about 85°F. male nymphs took about 38 days to mature, molting 3 times; females became adults after about 50 days, molting 4 times.

J. A. DOWNES. It would be remarkable if nutrient substances could pass through the wall of the oötheca. Did you indicate that this is the case?

L. ROTH. The oötheca of *Diploptera* is very thin and incomplete, covering only the basal halves of the eggs. It is believed by Hagan that the pleuropodia of the embryo, are involved in the transmission of nutriment from the female to the developing egg.